

Historical and ontogenetic changes in shell width and shape of land snails on the island of Kikai

Emiko Hayakaze¹ and Satoshi Chiba²

¹Institute of Geosciences, Shizuoka University, 836 Oya, Shizuoka 422, Japan

²Biological Institute, Graduate School of Science, Tohoku University, Aramaki-Aza-Aoba, Aoba-ku, Sendai 980-8578, Japan

Abstract: Patterns of change in shell width over a period of 35,000 years are documented in three fossil land snail species, *Euhadra pachya* (Pilsbry), *Phaeohelix phaeogramma* (Ancey), and *Coniglobus mercatorius daemonorus* (Pilsbry) on the island of Kikai in the Ryu-kyu Islands of the southwest part of Japan. The shell width of these species fluctuated through time, and the patterns were mostly synchronized among the three species. The temporal variations in shell width among fossil populations were far larger than geographical variations in shell width among modern populations. Since Kikai Island has been isolated from the other islands in the region, these morphological changes are regarded as genuine changes that have occurred within the island. The temporal changes in width were accompanied by distinct changes in spire index_j (height/width) within a single species. The patterns of change in width are correlated with the pattern of change in the climate since 35 Ka (35,000 years ago).

Key Words: body size, fossil, Kikai Island, land snail, shell morphology

A number of studies on the patterns and mechanisms of phenotypic evolution have been undertaken on fossil land snails in island systems (*e. g.*, Gould, 1969, 1984, 1989; Goodfriend and Gould, 1996; Chiba, 1996). Important contributions have been made to the study of patterns of Quaternary biogeographic change in island snails within an island (Goodfriend, 1987, 1993; Goodfriend and Mitterer, 1993; Goodfriend *et al.*, 1994; Cook *et al.*, 1993). In the present study, the morphologies of fossil and modern land snails from Kikai Island in the southwest part of Japan were studied, because it offers an excellent example to see morphological changes of lineages within an island.

Kikai Island, in the northern part of Ryukyu Islands, is a small island, approximately 60 km² in area and lower than 200 m above sea level. It has been isolated from other islands in the region since 100,000 years ago. The island has eolianite dunes that were produced during the late Pleistocene and Holocene no more than 40,000 years ago. Stratigraphic studies and ¹⁴C dating of the eolianite dunes on Kikai have been performed by Mitsui and Kigoshi (1966), Nakagawa (1967), Kakuta (1977), and Naruse and Inoue (1987), and these studies have shown that paleosoil layers have been produced four times: 32 - 31 Ka (thousand years ago) (period II), 29 - 27 Ka (period III), 22 Ka (period IV) and 3 - 2.5 Ka (period V). Fossil land snails have been reported from these paleosoil layers. In addition, land snail shells are found in a calcareous sand layer just above the base deposits of the dune. This layer consists of coarse

sand, blocks of beach rocks and marine shell fragments, and includes fossils of the land snails. The age of the snails from this calcareous sand layer is 35,600 yr (Naruse and Inoue, 1987), and the layer is designated period I. Fossil land snails are found in the dune deposits, and three species of pulmonates, *Euhadra pachya* (Pilsbry, 1902), *Phaeohelix phaeogramma* (Ancey, 1888), and *Coniglobus mercatorius daemonorus* (Pilsbry, 1901), are the most common species. *E. pachya* is endemic to Kikai, and *C. mercatorius daemonorus* is an endemic subspecies of Kikai Island.

Although it is not apparent how these species divide resources to avoid competition, *Phaeohelix phaeogramma* and *Coniglobus mercatorius daemonorus* seem to have similar niches: both live sympatrically under leaf litter or rocks on the ground and never climb trees. *Euhadra pachya* became extinct during the Holocene and so its habitat is not known. On the basis of observations of *E. herklotsi*, the most closely related species to *E. pachya*, it is assumed that the niche of this species is similar to that of *P. phaeogramma* and *C. mercatorius daemonorus*.

Here, we show evidence of distinct changes in shell width that have occurred in the three species during the past 35,000 years. The morphological patterns are synchronized among the three species. Distinct changes in shell shape follow the increase or decrease in shell width. Variations in shell shape may have close relationships with ontogenetic changes in shell shape (Foote and Cowie, 1988; Gould, 1984). We show that patterns of historical changes in shell

shape are associated with ontogenetic changes in shell shape. In addition, the correlates of climatic changes and other factors on the patterns of morphological changes are discussed.

MATERIALS AND METHODS

Twenty-two samples of fossil and living snails were collected from 18 localities (Fig. 1 and Table 1). Specimens used for the analysis were all adult snails that had a reflected, thickened shell lip. Specimens in each modern sample were taken from an area of 25 m². The vegetation at each modern site was categorized as shrub or forest (Table 1). Sites categorized as shrub were sites with plants lower than 1 m in height, and sites categorized as forest were sites with plants higher than 2 m in height. The leaf litter of the former was more than 30 cm in depth, but that of the latter was very thin. Forest and shrub did not coexist in a sampling site, because the area of each sampling site was small. All of the samples used in this study were deposited in Uni-

versity Museum, Shizuoka University (SUM).

Data of ¹⁴C ages previously reported for each layer are adopted for the age of the samples used in the present study (Table 1). These data were obtained by dating shells. In addition, the ages of seven fossil samples were examined by ¹⁴C dating. The ¹⁴C ages were determined by standard methods with benzene-liquid scintillation (Stipp *et al.* 1974; Gupta, 1985).

All fossil samples were collected from paleosol layers except for one sample (P16L) that was from the calcareous sand layer. *Phaeohelix phaeogramma* and *Euhadra pachya* were found in all fossil samples, but *Coniglobus mercatorius daemonorus* was not found in sample P16L. *E. pachya* was not found in the modern samples. In total, 951 specimens were measured. Characters measured were shell height (H), width (W) and number of whorls. An edge of the protoconch was defined zero whorls. Shell shape was represented by spire index (H/W) (Cain, 1977).

All three species examined here have determinate growth. Shell width and height at each whorl number (W_n and H_n in Fig. 2) were measured on the shell which was cut along the coiling axis. Ten snails randomly selected from the set of modern and fossil shells were cut in order to measure ontogenetic change for each species. Spire index at each whorl number was obtained by H_n/W_n, and ontogenetical changes of these characters were examined. In addition, relationships between shell width, number of whorls and spire index were examined in adult snails to estimate

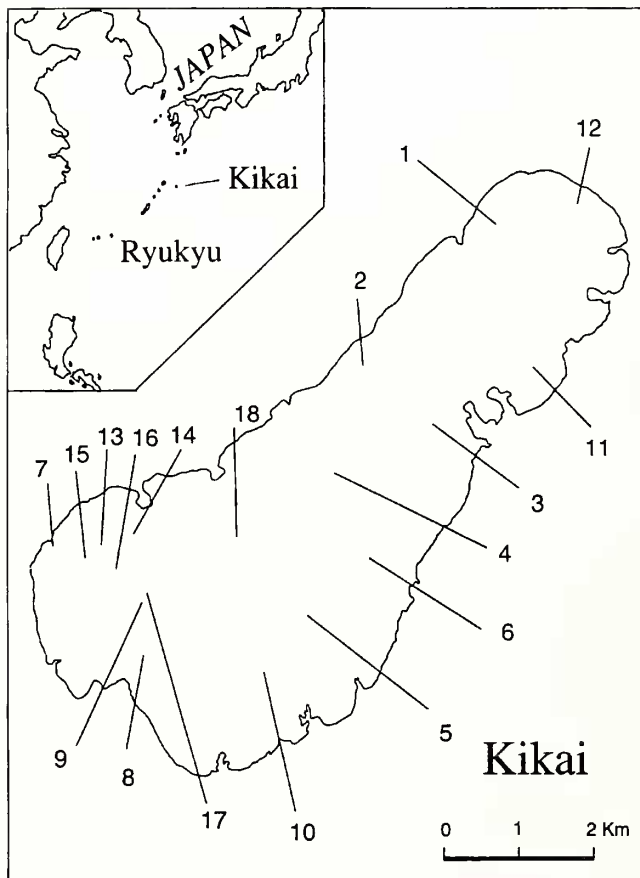


Fig. 1. Map of the island of Kikai showing the numbered sample locations.

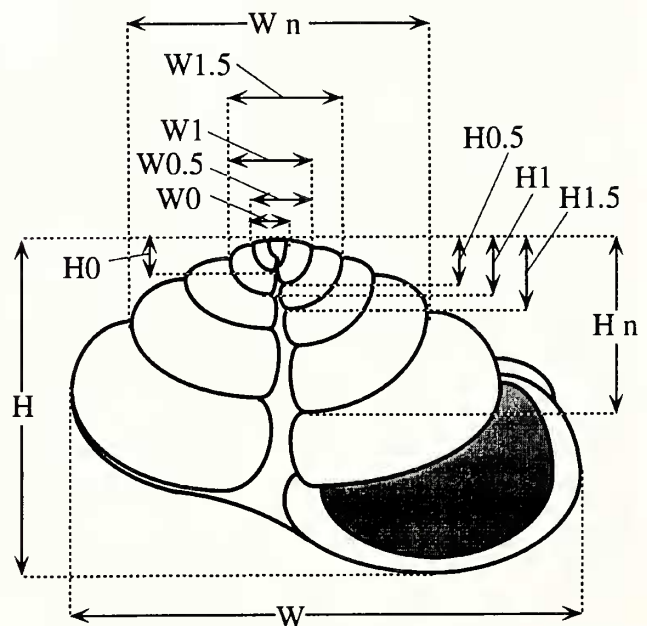


Fig. 2. Description of shell measurements on a cross section of a shell. W: width of an adult shell, H: height of an adult shell, W₀: width of a protoconch, W_n: width of the nth whorl (n=0.5, 1, 1.5, 2...), H₀: height of protoconch, H_n: height of the nth whorl (n=0.5, 1, 1.5, 2...).

Table 1. Modern and fossil samples of *Phaeohelix phaeogramma* (P.p.), *Coniglobus mercatorius daemonorus* (C.m.), and *Euhadra pachya* (E.p.) from Kikai (H=Holocene, P=Pleistocene, M=modern, U=upper section, M=middle section, L=lower section). Accession number of University Museum, Shizuoka University (SUMFC) for each sample is also presented. Asterisked ages are from Naruse & Inoue (1987). Vegetation and height above sea level for each sample site are also presented.

Loc.	Sample	Period	Age	Number of specimens			Vegetation	Height above sea level (m)	Accession number
				P. p.	C. m.	E. p.			
1	M1	Modern		22	13	0	forest	15	SUMFCC0051
2	M2	Modern		20	24	0	shrub	25	SUMFCC0052
3	M3	Modern		24	20	0	forest	8	SUMFCC0053
4	M4	Modern		20	30	0	forest	103	SUMFCC0054
5	M5	Modern		20	20	0	forest	150	SUMFCC0055
6	M6	Modern		20	12	0	forest	198	SUMFCC0056
7	M7	Modern		20	17	0	shrub	5	SUMFCC0057
8	M8	Modern		18	12	0	shrub	43	SUMFCC0058
9	M9	Modern		20	14	0	shrub	50	SUMFCC0059
9	P9	III	26800±500	46	16	28	unknown	50	SUMFCC0060
10	M10	Modern		25	21	0	shrub	55	SUMFCC0061
11	M11	Modern		21	10	0	forest	7	SUMFCC0062
12	H12	V	670±40	21	10	4	unknown	4	SUMFCC0063
13	H13	V	3030±90	24	5	6	unknown	15	SUMFCC0064
14	H14	V	3200±60*	36	12	15	unknown	14	SUMFCC0065
15	P15U	IV	22200±300	24	10	11	unknown	20	SUMFCC0066
15	P15L	II	31300±700	26	8	8	unknown	14	SUMFCC0067
16	P16U	III	27900±630*	10	10	8	unknown	32	SUMFCC0068
16	P16M	II	32600±870*	26	16	17	unknown	30	SUMFCC0069
16	P16L	I	35600±1500*	16	0	5	unknown	29	SUMFCC0070
17	P17	III	29100±400	45	18	22	unknown	46	SUMFCC0071
18	P18	II	31700±850	13	6	6	unknown	32	SUMFCC0072

effects of determinate growth of these species on their adult shell morphologies.

Geographical variation in shell width of the modern populations was examined to estimate the relationship between geographical variation in shell width and variation of local environmental conditions. Differences of shell width among modern samples were analyzed statistically with ANOVA. Temporal changes of shell width and spire index were examined by placing the populations in their stratigraphic context.

RESULTS

The ^{14}C age data presented in this study were consistent with the previous ^{14}C age data for the dune deposits of Kikai Island (Kakuta, 1977; Naruse and Inoue, 1987). ^{14}C age anomalies in snail shells were reported by Goodfriend and Stipp (1983) and Goodfriend (1987). Age anomalies in samples of living *Phaeohelix phaeogramma* and *Coniglobus mercatorius daemonorus* from Kikai have been examined and ranged from 300 to 800 years (Takahashi and Wada, 1998). This implies that the samples are 300 ~ 800 years younger than the ^{14}C ages, and that the order of ages of two samples in which the interval of ages is less than

1000 years is not clear. However, the affect of these age anomalies on the overall patterns of morphological changes are minor, because the intervals between most of the fossil samples examined in this study are greater than 1000 years except for those between the three Pleistocene samples (P15L, P16M, P18) and between the Holocene samples.

Shell width of the three species showed similar changes over the past 35,000 years (Fig. 3). Shells reached a maximum width at approximately 28 Ka, and stayed wide until 22 Ka. Specimens in samples H12 - H14 (2.6 - 3.2 Ka) were far smaller than the specimens of the sample P15U (22 Ka), indicating that a reduction in shell width had occurred between 22 and 3.2 Ka. The shell width of the modern samples was similar to that of samples from the Holocene deposits (2.6 - 3.2 Ka) and that of the samples during 29 - 35 Ka.

Because of the historical changes in shell width, the mean widths in some samples of *Phaeohelix phaeogramma* (28 ~ 22 Ka) were greater than the mean width of modern *Coniglobus mercatorius daemonorus*, which was approximately 1.2 times greater than the mean width of modern *P. phaeogramma*. In spite of the changes in width, however, the ratios of widths among *C. mercatorius daemonorus*, *P. phaeogramma* and *Euhadra pachya* within the same sample remained mostly constant. This constancy in ratios of width

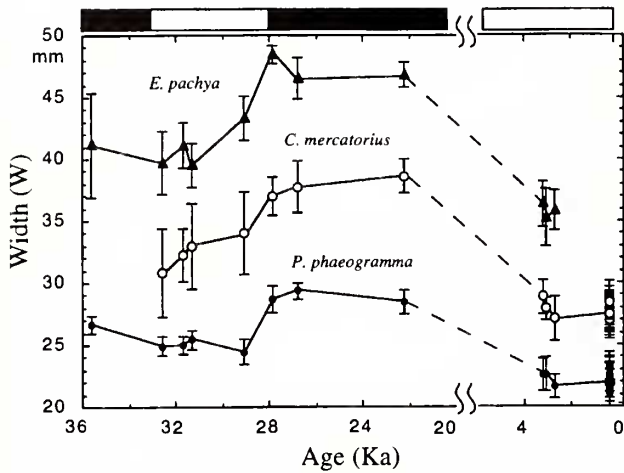


Fig. 3. Patterns of temporal change of sample means of shell width for three species through 35,000 years. Closed circles: *Phaeohelix phaeogramma*, open circles: *Coniglobus mercatorius daemonorus*, closed triangles: *Euhadra pachya*. Each bar indicates one standard deviation. The closed bar at top indicates periods of wetter climates than other periods.

resulted from simultaneous changes in width in the same direction in all three species.

The spire indices of *Coniglobus mercatorius daemonorus* and *Phaeohelix phaeogramma* also showed a pattern of change that was similar to that of shell width (Fig. 4). Spire index of the shells of *C. mercatorius daemonorus* increased at 28 Ka, and then it became low at 3.5 Ka. Spire index of *P. phaeogramma* also became low at 3.5 Ka. Especially, the spire index of modern *C. mercatorius daemonorus* is distinctly different from that of 28 - 22 Ka (Fig. 4). Within this species, the spire index of the modern sam-

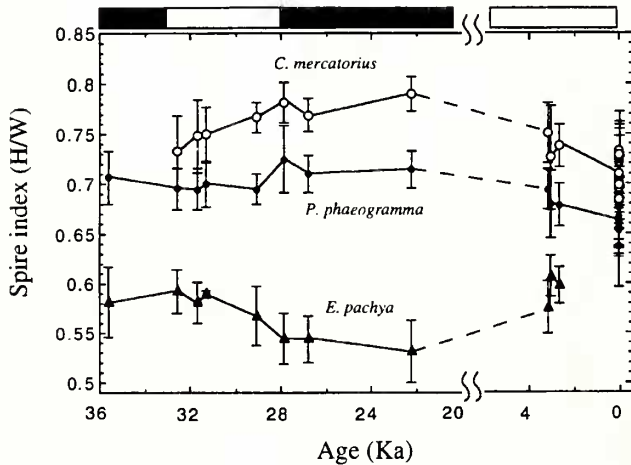


Fig. 4. Patterns of temporal change of sample means of spire index for three species through 35,000 years. Closed circles: *Phaeohelix phaeogramma*, open circles: *Coniglobus mercatorius daemonorus*, closed triangles: *Euhadra pachya*. Each bar indicates one standard deviation. The closed bar at top indicates periods of wetter climates than other periods.

ples and those of the fossil samples before 28 Ka were closer to each other than the samples of other ages (Fig. 4). *Euhadra pachya* also showed temporal changes in spire index, but the specimens in the fossil samples from 28 Ka to 22 Ka had a lower spire index than the samples of other ages (Fig. 4).

Ontogenetic changes of spire index showed that the spire index (H_0/W_0 , $H_{0.5}/W_{0.5}$, H_1/W_1 ... H/W) of *Coniglobus mercatorius daemonorus* and *Phaeohelix phaeogramma* decreased from juvenile to middle stage (whorl numbers fewer than 3), but increased after the middle stage (Fig. 5). However, the spire index of *Euhadra pachya* monotonically decreased during ontogeny (Fig. 5). All of the specimens of a species showed consistent ontogenetic patterns. A similar pattern is seen in spire index versus width.

There were nearly perfect correlations among width, number of whorls and spire index of adult shells (Fig. 6). There was a positive correlation between shell

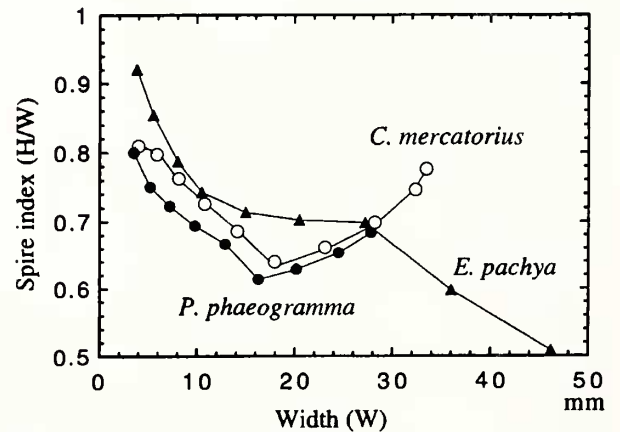
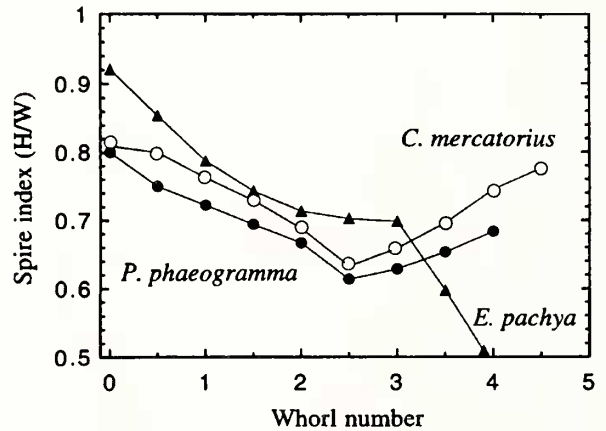


Fig. 5. Ontogenetic changes of spire index versus whorl number and shell width for representative specimens of the three species. Closed circles: *Phaeohelix phaeogramma*, open circles: *Coniglobus mercatorius daemonorus*, closed triangles: *Euhadra pachya*.

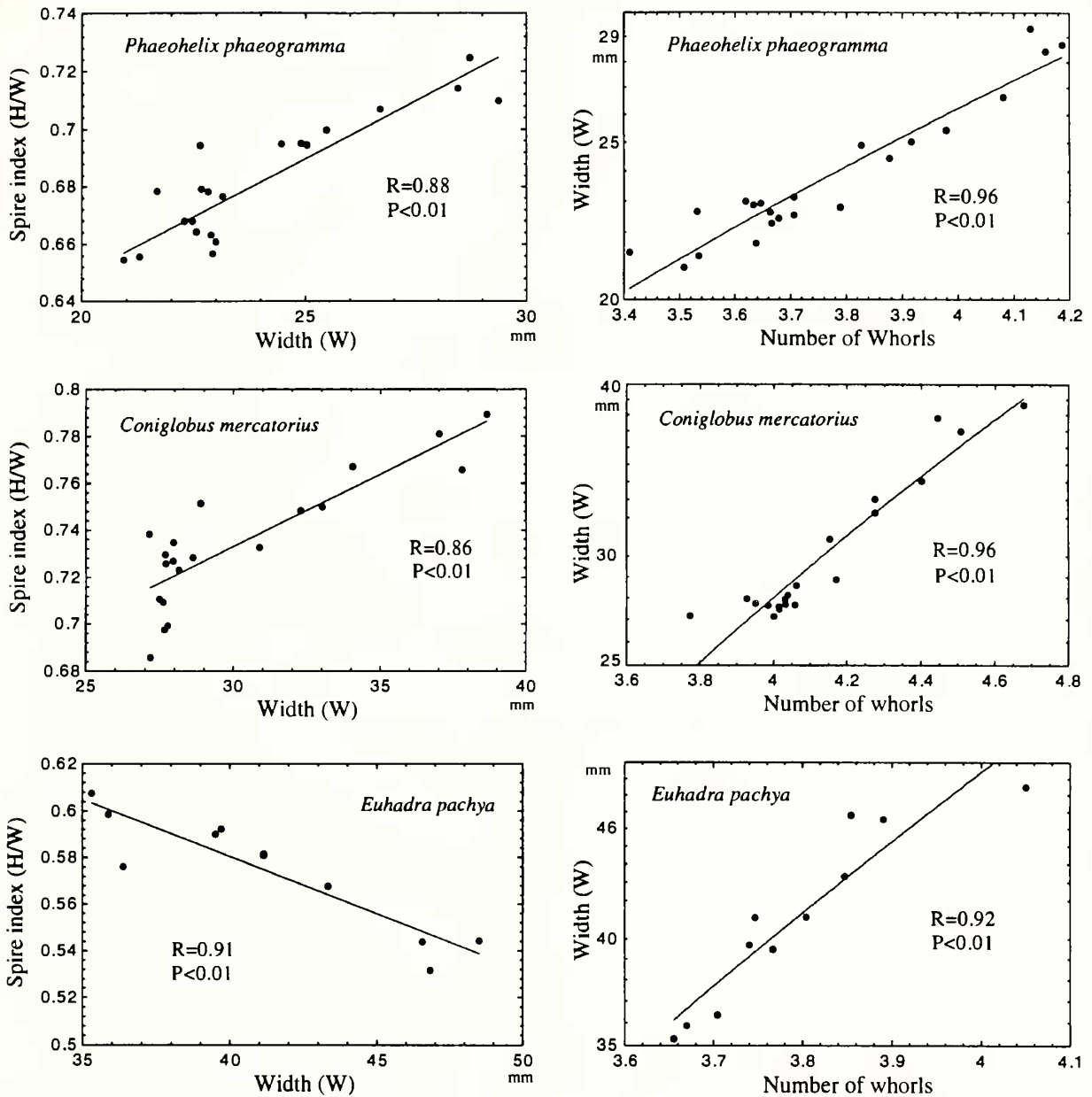


Fig. 6. Relationships among sample means of adult shell width (W), spire index (H/W), and number of whorls. A positive correlation between the number of whorls and the width is found in all species. A positive correlation between width and spire index is found in *Phaeohelix phaeogramma* and *Coniglobus mercatorius daemonorus*, but that of *Euhadra pachya* shows a negative correlation. Correlation coefficients (R) and P values are shown.

width and the number of whorls in the three species. *Coniglobus mercatorius daemonorus* and *Phaeohelix phaeogramma* showed a positive correlation between width and spire index. *Euhadra pachya* had a negative correlation between width and spire index. Correlation coefficients for these relationships (see Fig. 6) were all statistically significant ($P<0.01$ in all cases, see Fig. 6).

Geographical variations in shell width observed in the modern samples of *Phaeohelix phaeogramma* are shown in Fig. 7. Shell widths of samples M8, M9, and M10

collected from shrub were significantly smaller than all of the samples collected from forest ($P<0.05$). Shell width of sample M2 from shrub did not differ significantly ($P>0.05$) from any forest samples except sample M6 ($P<0.05$), and sample M7 from shrub did not differ significantly from any of the forest samples ($P>0.05$). As a whole, however, shell widths of snails from forest tend to be larger than those from shrub. Two modern samples of *Coniglobus mercatorius daemonorus* (M9 and M10) from shrub had statistically smaller shell widths than samples from forest ($P<0.05$),

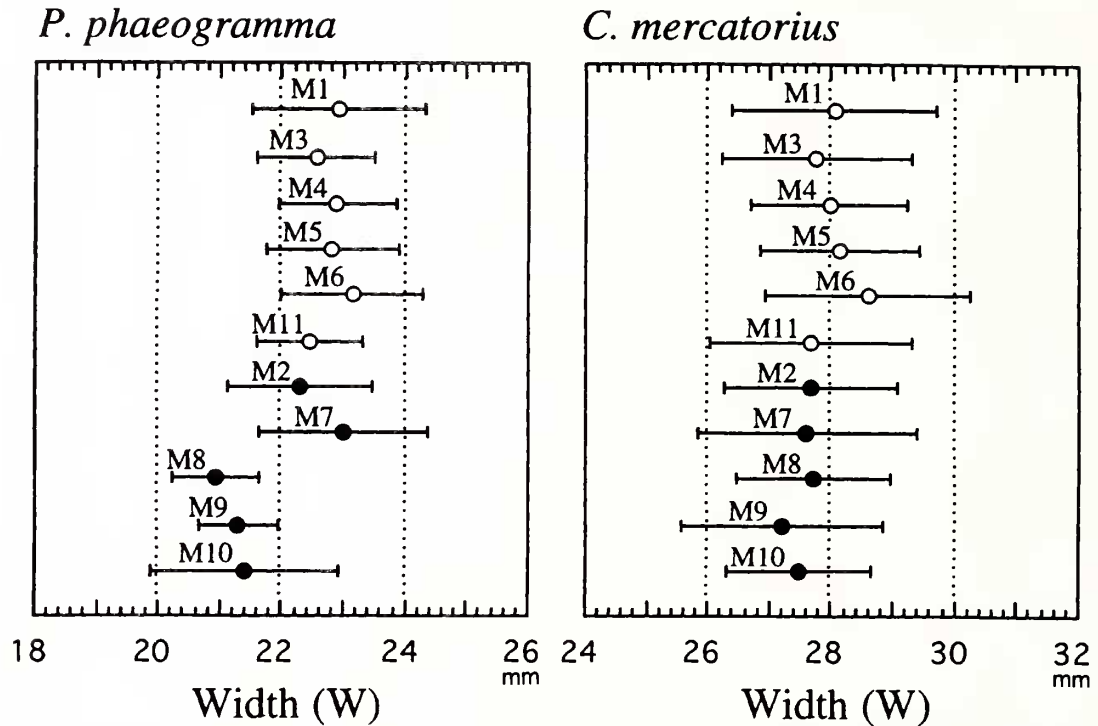


Fig. 7. Geographical variation in sample means of shell width among modern samples of *Phaeohelix phaeogramma* and *Coniglobus mercatorius daemonorus*. Open circles: samples collected from forest, closed circles: samples collected from shrub. Each bar indicates one standard deviation.

but shell width of other samples from shrub did not differ significantly from forest samples ($P > 0.05$).

A significant association of shell width and the height above sea level of the modern sampling site (correlation coefficient $R = 0.70$, $P < 0.05$) was found in *Coniglobus mercatorius daemonorus* (Fig. 8). However, the scatter is wide and the significance is probably dependent on only a few of the outlying points. In addition, association of these was not clear in *Phaeohelix phaeogramma* ($R = 0.28$, $P > 0.05$).

DISCUSSION

The synchronized patterns of change in shell size and shape of *Euhadra pachya* and *Coniglobus mercatorius daemonorus* are regarded as genuine changes that have occurred within the island and not a reflection of migration within the island or from elsewhere, because these species are endemic species and subspecies respectively, and because the morphological variation among the modern populations was far smaller than that among samples with different ages. Because Kikai Island has been isolated from other islands since the last ice age (Nakagawa, 1969), the pattern of change documented in *Phaeohelix phaeogramma* also does not reflect immigration from other areas.

The morphological patterns showed that shell width of *Phaeohelix phaeogramma* seemed to decrease during 36 - 32 Ka. Shell widths of the three species remained low during 32 - 29 Ka, and increased after 29 Ka, and reached maximum during 28 - 22 Ka. This latter period corresponds to the time when sea level was lowest. Although there is no fossil record for the period 22 - 4 Ka, reduction of shell width occurred during this period when sea level rose. Yasuda (1987) has suggested that the Japanese islands were wetter 50 - 33 Ka and 28 - 25 Ka than other periods. Although climate of the main parts of the Japanese islands became slightly dry after 25 Ka, the relative increase of the land height of Kikai (approximately 100 m) due to the fall of sea level during 28 - 20 Ka may be responsible for the wettest climate in the island during this period. The periods with wet environments (50 - 33 Ka and 28 - 20 Ka) roughly correspond to the periods when shell width was larger (periods older than 32 Ka and 28 - 22 Ka). Thus, increased shell width appears to be correlated with wet conditions.

There are many environmental factors that can affect shell size, e. g., moisture, temperature, density, predation, and random effects, but temperature and moisture may be the most important factors (Goodfriend, 1986; Emberton, 1994). Moisture level is the best documented environmental correlate of shell size, and a positive correlation between moisture and size or aperture area has been

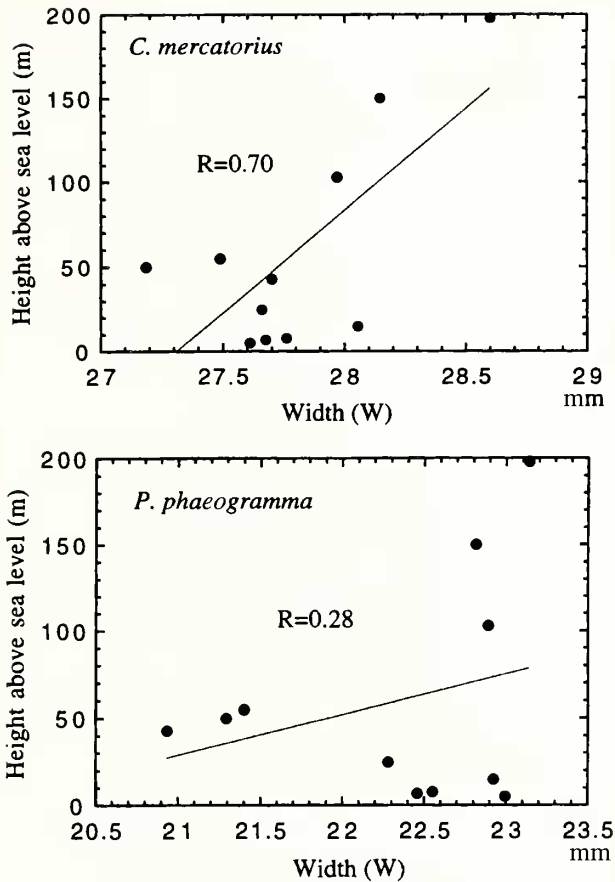


Fig. 8. Relationship between mean shell width of a sample and the height above sea level for samples of modern *Phaeohelix phaeogramma* and *Coniglobus mercatorius daemonorus*.

reported by many authors (e. g., Rensch, 1932; Heller, 1975, 1979; Goodfriend, 1986; Emberton, 1994). In this study, larger shell widths of living snails from forest than from shrub suggest a similar relationship with moisture. The correlation of the morphological pattern with the supposed pattern of climatic change suggests that the historical change in shell width may have been induced by the climatic change.

There are several possible processes by which environmental changes could induce changes in shell width. These changes may be ecophenotypic responses to the changing environment. Distinct non-genetic changes in shell morphology can be created by environmental changes without genetic changes (Gould, 1984). However, these changes may be genetic and evolutionary changes. Breeding experiments on a number of land snail species have shown that size differences among populations have a high heritability (Cook, 1967; Murray and Clarke, 1968; Cook and Cain, 1980; Johnson *et al.*, 1993). Cain (1977) suggested that natural selection for differences in feeding behavior have resulted in divergence of shell height (and see Cook

and Jaffar, 1984; Heller, 1987; Emberton, 1994). It is difficult to determine whether the observed changes are genetic or non-genetic. Regardless of the basis of the changes, however, the relationship of climate and shell morphology in the history of these land snail species is affirmed.

There are at least two possible causes for the patterns of historical changes in spire index. First, these changes may reflect adaptation for environmental conditions. Shells with high spires are adaptive in environments with high humidity, because high moisture conditions permit more diverse foraging activities and should mechanically favor higher spires (Cain, 1977; Emberton, 1994). However, in the present examination, shells with a high spire index were not necessarily found in the fossil samples of the period with wet environments. For examples, shells of *Euhadra pachya* became flatter during the period with wetter environments.

Second, these changes may reflect ontogenetical relationships among characters. There was a nearly perfect correlation between shell width and number of whorls, and this relationship implies that a larger shell is a shell with more whorls. Climate affects the number of whorls or shell width at which growth ceases, thereby affecting spire index. A species that increases its spire index with increasing number of whorls and shell width after the middle stage produces an adult shell with low spire index by becoming adult at a reduced number of whorls, thereby decreasing shell width. Therefore, patterns of change in spire index can be interpreted as by-products of the change in numbers of whorls and shell width because of the correlation between width and spire index that is determined ontogenetically. A positive or negative correlation between spire index and shell width observed in the samples of adult snails reflects this ontogenetical relationship between characters.

A positive correlation between spire index and shell width in *Phaeohelix phaeogramma* and *Coniglobus mercatorius daemonorus* and a negative correlation between these parameters in *Euhadra pachya* imply that the high spire index of *P. phaeogramma* and *C. mercatorius daemonorus* and low spire index of *E. pachya* of 28 ~ 22 Ka were created by increasing the shell width by increasing the number of whorls (Fig. 6). The temporally fluctuating patterns of shell shape presented in this study may be induced by fluctuations of shell width that are induced by climatic change.

A correlation between spire index and shell width is found in most land snails (e. g., Goodfriend, 1986). It has been claimed that a non-adaptive change of morphology can occur when the characters are closely linked to size (Gould, 1966, 1969, 1971, 1984). For example, heterochrony, an important cause of evolutionary novelty (Gould, 1977; McKinney, 1986), could produce shape variations as a result of a change in size or a change in the time to maturation. The present study suggests that temporal change in shell

form can occur in association with a change in shell width. This idea implies that changes in shell form of the three species could simply be a direct consequence of a change in number of whorls, and may not be adaptive. Although it is difficult to demonstrate that they are non-adaptive at present, the presence of opposite trends in species with similar life styles suggests that the occurrence of non-adaptive change in shell shape can not be ruled out.

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